On the Post-Embryonic Development of certain Chalcids, Hyperparasites of Aphides,

with Remarks on the Bionomics of Hymenopterous Parasites in General.

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With 7 Text-figures.

Introduction.

In the summers of 1919 and 1920, certain hyperparasitic Chalcidoidea were reared from material collected in the field for the study of two hyperparasites of aphides, the Proctotrypid, Lygocerus (**5**), and the Cynipid, Charips (**6**).

The following is an account of the post-embryonic development of two common forms, which were obtained in considerable numbers from the cocoons of the Braconid, Aphidius ervi, Hal., a parasite of Macrosiphum urticae, Kalt., an aphid that infests the stinging nettle.

I would here express my sincere thanks to Professor Stanley Gardiner, who gave me facilities to carry out the work in the Zoological Laboratory, Cambridge; and to Mr. J. Waterston of the British Museum (Natural History), who kindly determined the species of Chalcidoidea submitted to him.

Bionomical and Systematic Position.

The two species now considered belong to the sub-family Sphegigasterinae of the family Pteromalidae, which is, according to Ashmead, the largest group of the Chalcidoidea, and the most difficult to classify.

Asaphes vulgaris, Wlk., belongs to the tribe Asaphini, the majority of which are said by Ashmead to be parasitic on Aphidiidae and Coccidae (**1**).

Pachycrepis clavata, Wlk., is included in the allied tribe Pachyneurini, which Ashmead says are regarded as chiefly parasites of the same Rhynchota, but he adds that these insects have other hymenopterous parasites, through which the Pachyneurini are probably hyperparasitic.

In addition to Asaphes and Pachycrepis, two females of a species of Pachyneuron were reared. The eggs and early larval stages of the two former species are indistinguishable. The egg of the Pachyneuron is characteristic, but its development was not observed.

Various Chalcidae have been recorded as reared from aphides, and it is possible that some of them may yet prove to be primary parasites; but the forms described here are hyperparasites of the plant-lice through the larvae of Aphidius, and allied genera of Braconidae, which develop internally in aphides. The Chalcidae do not oviposit until the aphid is dead and the Aphidius has woven its cocoon, and is ready to transform inside the empty skin of its late host. Their true relation to the aphid was shown as long ago as 1834 by Nees ab Esenbeck for Asaphes or a similar form, and his observations have been confirmed by Walker and Buckton, and subsequently by other writers.

These hyperparasites do not appear to be specific for different Aphidiidae or aphides. In 1919 I reared Asaphes vulgaris from an Aphidius in Rhopalosiphum sonchi, Kalt., and also from Aphidius salicis, Hal., a parasite of Aphis saliceti, Kalt. This Braconid and aphid are less than half the size of A. ervi and M. urticae, but the Chalcid seems to adapt itself to either form, and thus probably has considerable latitude in the choice of a host.

PAIRING.

All observed ovipositions of Asaphes and Pachycrepis took place after pairing. Only two examples of Pachyneuron were obtained, and both were females.

One laid a single egg parthenogenetically and died soon afterwards. The other lived for some days but did not oviposit.

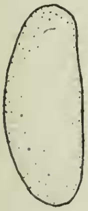
OVIPOSITION.

The female Chalcid selects a cocoon containing an Aphidius larva on the point of metamorphosis, but sometimes a newly-transformed pupa may be chosen. The hyperparasite shows considerable excitement in her search, and runs round the cocoon, tapping it eagerly with her antennae. Finally she mounts upon it, facing the head of the aphid, and, boring through the integument with its silk lining, she deposits a single egg upon the upper surface of the body of the Aphidius larva, as it lies curved head to tail within the cocoon. The whole operation lasts from one to three minutes. Only one egg is inserted at each oviposition, and when more are found they are the result of different attacks. The number of eggs laid by each female seems to be between thirty and forty, but it is difficult to be precise on this point as the insects will live for some days in captivity, and the eggs in the ovarian tubes do not all mature at the same time.

THE EGG.

The eggs of Asaphes and Pachycrepis are indistinguishable from one another. They are white, elliptical bodies with a smooth chorion, having dimensions, ·29 × ·12 mm. (Text-fig. 1).

TEXT-FIG. 1.



Egg of Asaphes vulgaris.
×100.

TEXT-FIG. 2.

Egg of Pachyneuron sp.
×100.

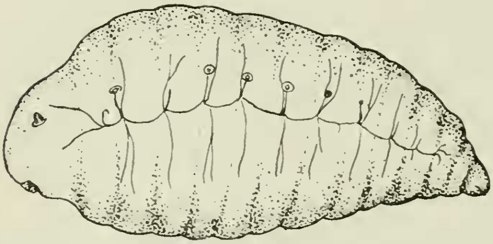
The single example of the egg of Pachyneuron was long, oval, and slightly curved. On the concave side, the chorion is smooth, but the rest of the surface is covered with minute scales or papillae. Dimensions, ·31 × ·10 mm. (Text-fig. 2). This egg is very similar to that of Pachyneuron gifuensis, Ashm., figured by Howard and Fiske (7).

The First Instar.

Dimensions ·45 mm. × ·23 mm.

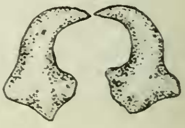
The egg hatches about sixty hours after oviposition. The larva in the first instar much resembles in general form that of the Lygocerus previously described (Text-fig. 3). It is white, semi-transparent, and consists of thirteen segments in addition to the head, which is furnished with two tactile papillae. The mouth is small and oval, and the mandibles are somewhat more curved than those of the larva of Lygocerus (Text-fig. 4).

Text-fig. 3.



The larva of the first instar. ×300.

Text-fig. 4.



Mandibles of the newly-hatched larva. ×600.

The tracheal system consists of a pair of longitudinal trunks, united by an anterior commissure between the first and second segments, and a posterior commissure in the eleventh segment. At this stage there are four pairs of functional spiracles, namely between the first and second segments, and on segments 4–6 inclusive. These segments are supplied with dorsal and ventral lateral branches, and the developing spiracular trunks of segments 3 and 7–9 are visible. The larva makes an incision in the skin of the host, and as the body-fluids of the latter fill the midgut the hyperparasite is tinged pale yellow.

INTERMEDIATE STAGES.

The exact number of ecdyses of these Chalcids was not determined. There is no marked change of form during development, but the body becomes more globose, and the head less conspicuous. The cephalic papillae do not disappear as in Lygocerus, but persist until metamorphosis. The spiracles on segments 7 and 8 become functional, and those on segment 3 open shortly afterwards. The ninth pair (on segment 10) open as development proceeds, but the tenth pair are closed until shortly before metamorphosis.

The host dies a day or two after the Chalcid larva has begun to feed, and decomposes rapidly. These hyperparasites penetrate more deeply into the decaying tissues than do the larvae of Lygocerus at the same stage. The larvae are also more fragile and transparent, and are easily crushed or ruptured when handled.

THE FULL-GROWN LARVA.

Dimensions, 1·26 mm × ·60 mm.

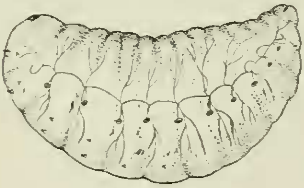
The larva when fully fed is creamy white and opaque, slightly curved, and with a smooth glabrous cuticle. The body tapers somewhat to the anus, and the segmentation is well marked. The head bears a pair of conspicuous papillae, and a pair of similar, though smaller, appendages are found on the first segment. In addition, each segment from the first to the fifth or sixth is furnished with one or two pairs of minute spines (Text-fig. 5).

The labrum and labium both bear palps, as do also the maxillae. The mandibles are simple, and strongly chitinized, though less massive than in Lygocerus (text-fig. 6).

The ramifications of the tracheal system are more elaborate than in the preceding stages, and the tenth spiracle (on segment 11) becomes functional.

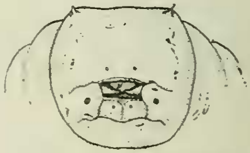
The internal structure is of the type usual among hymenopterous larvae. The narrow oesophagus opens by a valve into the vast mesenteron filled with food, which is churned to and fro by muscular contractions. The mesenteron is closed posteriorly and does not communicate with the proctodaeum until immediately before metamorphosis. A pair of short Malpighian tubules enter the hindgut at its anterior end. The salivary glands extend backwards to the ninth segment, and lie on either side of the gut ventrally as a pair of long straight tubes. Behind the head their ducts unite to form the common salivary duct, which opens on the floor of the mouth. The ventral nerve-cord appears as a broad unconstricted band extending backwards into the tenth segment. The rest of the internal structure calls for no particular comment.

TEXT-FIG. 5.



The full-grown larva. ×25.

TEXT-FIG. 6.



Head of the full-grown larva. ×75.

In a cocoon opened carefully when the hyperparasite was almost full grown, it was possible to watch the transformation into the pupa, and by this means it was determined that the mature larvae of the two forms examined were identical in appearance. Attempts to follow the earlier development in the same way always failed, because exposure to the air caused the decaying tissues of the Aphidius to dry up and thus brought about the death of the hyperparasite. The larval development of the Chalcidoidea has been more studied than that of other Hymenoptera parasitica, but so much diversity exists within the family, owing to secondary modifications induced by various hosts and habits, that a comparative account can throw little light on their affinities. The forms here described agree very closely with that of Torymus propinquis, an ectoparasite of certain Cecidomyiidae, studied by Seurat (**10**). The general form and the number and order of opening of the spiracles are the same in both cases. Certain parasites of Coccidae, described by Imms (**8**) show a reduction in the number of spiracles from behind forwards; but in one, Aphycus melanostomatus, rudimentary trunks of the tenth pair appear during development, though they never become functional. Ectoparasitic Chalcidae, such as Asaphes and Torymus, have probably retained certain primitive features, such as the full number of spiracles, which have been lost in the more specialized and frequently hypermetamorphic forms, found among the endoparasitic members of the super-family.

Pupation and Emergence.

When the remains of the Aphidius have been completely devoured, the gut of the hyperparasite opens, the meconium is voided, and the Chalcid pupates within the cocoon previously woven by the Aphidius inside the skin of the aphid. The pupal stage lasts from fourteen to sixteen days, for Asaphes and Pachycrepis; but in a single observed instance of Pachyneuron the period of pupation was only ten days. When ready to emerge, the imago gnaws a hole in the cocoon and creeps out. The adults lived in confinement for from four to seven days, and fed on the sap oozing from cut leaves, and on honey-dew which had fallen from the aphides.

At least two generations may occur in the year, but the exact number was not ascertained: it is probably dependent on the number of hosts obtainable. There is no evidence to show how these Chalcids pass the winter.

Remarks on the Bionomics of Hymenopterous Parasites in General.

The relations of any animal to its enemies, predatory or parasitic, form what may be termed a bionomical complex; although the limits of such a complex are often difficult to determine, especially when the enemy has a wide choice of alternative food or host species.

Aphides, with their parasites and hyperparasites, form a bionomical complex of considerable intricacy; but its limits are well defined, and it is thus convenient for the study of the bionomics of parasitism. The Aphidiidae, which are a large and distinct sub-family of Braconidae, are all obligative parasites of Aphides, and have no alternative hosts; and the hyperparasites, which belong to the three super-families of Cynipoidea, Chalcidoidea, and Proctotrypoidea, are exclusively confined to the Aphidiidae, with the exception of certain Cynipids (Charipinae) and Chalcids, which possess allied forms parasitic upon Coccidae.

The bionomics of some members of this complex are comparatively simple. Thus, the species of Charips (Cynipidae) described elsewhere (**6**) are invariably parasites of Aphidius, and thus hyperparasites of the aphid, and, so far as is known, never prey upon another hymenopteron. The status of such Proctotrypids as Lygocerus (**5**), and Chalcids such as Asaphes and Pachycrepis, is more difficult to determine, because although usually parasites of Aphidius, and therefore standing in the same relation to the aphid as Charips, they may on occasion be parasitic on each other. The interrelations of these forms are shown in the accompanying diagram (Text-fig. 7). An Aphidius cocoon is sometimes found to contain two hyperparasites of either, or both these species, the result of two successive ovipositions. Fiske (**3**) has called this phase of parasitism 'superparasitism'; but as the word means neither more nor less than hyperparasitism, a term already employed in cases where the parasite is itself attacked by a parasite, I would suggest replacing this etymological hybrid by 'epiparasitism'. In such a case, in the aphid complex, only one imago emerges from the cocoon. Either one parasite is sufficiently advanced to devour the host before its rival can compete with it; or else, if both parasites are of the same age, there is insufficient food to nourish both up to metamorphosis, and they starve to death. One seems never to make a direct attack on the other.

But in certain instances a Chalcid hyperparasite larva, generally one three-quarters grown, may be found with the egg or larva of a Proctotrypid, or of another Chalcid, on its body. It may be that the second hyperparasite deliberately oviposits upon the larva of the first, if the Aphidius host has already succumbed to the attack, and originally I thought that this was the case: but further observation led me to modify this conclusion. Thus instances of this kind are rare compared with those of simple epiparasitism and attempts to induce the Chalcid or Proctotrypid to oviposit on the full-grown larva of another hyperparasite that had already devoured

TEXT-FIG. 7.

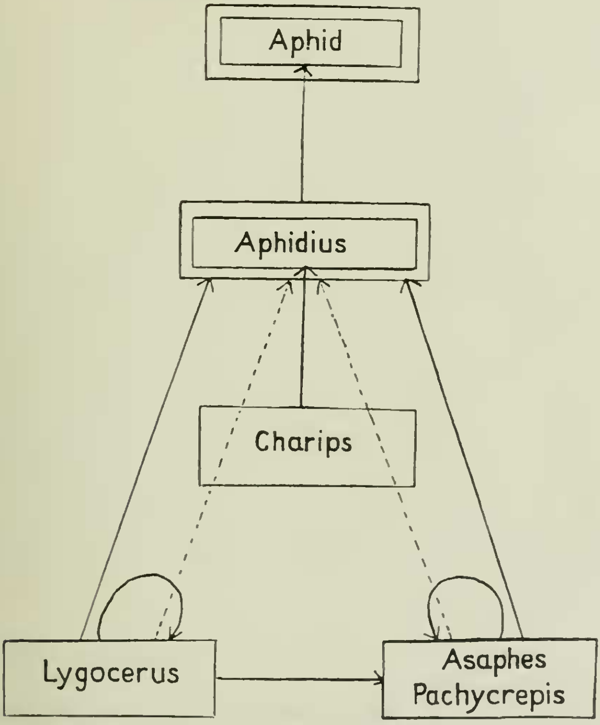


Diagram to illustrate the bionomical complex of an aphid, its parasites, and hyperparasites. Endoparasitism is indicated by a double margin to the host.

the host, always failed. The more probable explanation seems to be that the intention of the second hyperparasite is to oviposit upon the Aphidius, but if by chance her ovipositor comes in contact with the larva of the first, she is unable to distinguish between it and the proper host, and places her egg upon it. Certain observations support this view. For instance, young larvae were never found thus parasitized, possibly because they escaped discovery owing to their small size; and the mature larva of Lygocerus was never found to be infected. There is very marked increase in the size in this species between the early and late stages, and the latter is of peculiar form with a dorsal conical appendage to the last segment. The full-grown larva and the pupa are capable of active movement, and jerk the abdomen violently when irritated. It is possible that this action warns off the ovipositor of another hyperparasite. I have observed only three instances where Lygocerus was parasitized, and then always by its own species. In two cases, larvae were observed on newly-transformed pupae, and here, contrary to the usual rule, the egg must have been placed on the larva when nearly full grown. In the third case, an egg was found upon a younger larva, whose power of movement was not yet developed.

The Chalcid larvae, which are sluggish at all stages, are more frequently attacked in their later instars by Lygocerus and by other Chalcids.

The incidence of mortality from epiparasitism is high in the Cynipidae, since they invariably perish within the host when the latter is attacked by an ectoparasite. Exceptionally, a full-grown larva of Charips may be found epiparasitized by a Chalcid or by Lygocerus, and in such cases it is probable that the oviposition of the second hyperparasite coincided with the emergence of the Cynipid from the host, and before it had demolished the remains of the latter.[1]

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[1] It should be pointed out that other forms not dealt with here are involved in this bionomical complex. Thus Silvestri ("Contribuzioni alla conoscenza biologica degli Imenotteri Parassiti", 'Boll. Lab. Scuola Agric. Portici', vol. iii, 1909) has described the development of a Chalcid,

It is clear that this phase of parasitism differs somewhat from ordinary epiparasitism. It has been called ‘ accidental superparasitism ’ by W. D. Pierce, quoted by Fiske (**3**), but might better be termed ‘ metaparasitism ’. Epiparasitism then may be defined as successive infestations of a single host by two or more species, or by several individuals of the same species, of parasite. Metaparasitism is a development of epiparasitism, and may be defined as the direct attack of one epiparasite upon another. Objection may be taken that the distinction is too fine to warrant the coining of a new word in a science already burdened with technical names ; but of late years the practice of introducing parasites to control insect pests, in countries or continents where the latter have become troublesome, has been much extended ; and, before importing a parasite into a new area, it is of the first importance to ascertain to what extent it is potentially metaparasitic upon other species.

Thus, suppose that two forms of primary parasites A and B are imported into a certain locality. There will be a slight reduction of their total efficiency, in proportion to the incidence of epiparasitism between them ; but as long as plenty of hosts are available, the loss due to this will be small, and in any case little harm will result, as a pest destroyer will be reared ultimately. But supposing that B is potentially metaparasitic, while A is not, then in course of time. B. since it will always be successful in contest with A, will reduce the latter species, or even supplant it altogether. The mischief will be even greater from an economic standpoint, if B should prove to be less efficient than A in destruction of the host pest.

In fact, this is what has actually taken place in Hawaii.

Eucyrtus aphidivorus, Mayr., which like Charips is an endoparasite of Aphidius ; but as its other bionomical relations are not known, it has not been included in this discussion, and the same applies to other Chalcidae, recorded as reared from Aphides, but many, if not all of which, are probably hyperparasites. However, as Arrow (‘ Entomologist’s Monthly Magazine ’, vol. lvii, September 1921) observed Aphelunis chaonia, Wlk., ovipositing in aphides, this form may prove to be a primary parasite.

according to the recent investigations of Pemberton and Willard (**9**). Among the parasites introduced to control the Mediterranean fruit-fly (Ceratitis capitata, Wied.) were two species, Opius humilis, Silvestri, and Diachasma tryoni, Cameron. It has now been shown that epiparasitism is common between Opius and Diachasma, and that in such a case Diachasma is nearly always victorious. Thus Diachasma is gradually suppressing Opius in Hawaii; and, as the authors point out, this result is the more deplorable in that Opius is not only equally efficient as a parasite, but is actually more prolific than its rival, and if left to itself would destroy a larger number of fly larvae. The situation has been further complicated by the introduction of a Chalcid, Tetrastichus giffordianus. This form is very prolific; but, as it is almost always epiparasitic, it is ineffective as a control of the pest, and generally causes the death of the Opius or Diachasma larva when it comes into competition with them.

Fiske and Thompson (**4**) have shown that the larvae of certain Saturniidae are parasitized by the hymenopterons, Ophion, Theronia, and Spilocryptes. All three are primary parasites, but epiparasitism is frequent, and when it occurs, Theronia and Spilocryptes respectively overcome Ophion. In competition between Spilocryptes and Theronia, the first generally is the conqueror; but Theronia, it appears, dies of starvation from destruction of its food-supply rather than by direct attack.

Timberlake investigated the bionomics of Coccophagus lecanii, Fitch (**14**), a parasite of Coccus hesperidum, which is more frequently reared as a hyperparasite from another primary parasite, Microterys. According to this observer, Coccophagus is thelyotokous when a primary parasite, producing generations of females only; but when it is reared as a hyperparasite, the resulting imagos are all males—a state of things so far unparalleled.

Howard and Fiske (**7**) in their report on the measures taken to control the gipsy and brown-tail moths in the United States, record many interesting observations on the bionomics of native and imported parasites. Thus the Chalcid Schedius Kuvanae, How., is primarily an egg parasite of the gipsy moth, but it will also oviposit in Anastatus bifasciatus, Forst., another egg parasite. In this complex, two other species, Tyndarichus novae, How., and Pachyneuron gifuensis, Ashmead, are hyperparasitic upon Anastatus, but epiparasitism is frequent, and they have been reared not only from Schedius, but also from one another.

Monodontomerus aereus, Walk., and Pteromalus egregius, Forst., are also primary parasites of the gipsy moth and brown-tail moth respectively; but both forms are also hyperparasitic through certain Tachnidae, and, in addition, the latter form is sometimes reared from other hymenopterons, such as Mesochorus and Apanteles.

Smith (**12**) has shown that Perilampus hyalinus, Say., although strictly speaking an obligative hyperparasite of certain lepidopterous larvae, through their hymenopterous and dipterous parasites, may, when epiparasitism occurs, become metaparasitic. Thus in one instance a cocoon of the Ichneumonid, Limnerium validum, was first parasitized by Perilampus, and subsequently by the Pteromalid Dibrachys boucheanus. The latter devoured the Limnerium host, but was shortly afterwards itself destroyed by Perilampus.

The following table gives the synonyms used by previous writers on the bionomics of the Hymenoptera parasitica for the terms suggested here.

Parasitism	Primary parasitism. Parasitism.
Epiparasitism	Superparasitism. Secondary parasitism. Secondary hyperparasitism.
Metaparasitism	Accidental superparasitism. Tertiary hyperparasitism. Superparasitism.
Hyperparasitism	Secondary parasitism. Hyperparasitism.

These terms may be illustrated with examples from the aphid complex as follows:

Parasitism	aphid+Aphidius	
Epiparasitism	aphid+Aphidius+	Lygocerus and Asaphes
Metaparasitism	aphid+Aphidius+	Asaphes+Lygocerus
Hyperparasitism	aphid+Aphidius+	Asaphes or Lygocerus or Charips

The possibility of 'hyper-hyperparasites' has been suggested by some writers, but although obligative hyperparasitism of the second degree may occur, I am not aware that it has been definitely proved. The records that seem to point to it are probably due to epiparasitism among hyperparasites.

Apart from their economic importance, cases such as those described are of much biological interest, as throwing light on the origin of parasitism in the Hymenoptera parasitica.

Thus the epiparasitism of Lygocerus and Asaphes may exceptionally become metaparasitism, if, by chance, one species oviposits directly upon the larva of the other; and a stage further has been reached in Coccophagus and Theronia which are as often hyperparasites as parasites. Fiske says of the latter (**3**) that it is so frequently a 'superparasite' that it is in danger of becoming a hyperparasite. From such forms as these it is not a great step to the obligative hyperparasitism of, for example, Charips.

Epiparasitism is brought about by a high proportion of parasites to the host population. Fiske (**3**) has made an ingenious calculation, showing that as the incidence of parasitism rises, the chances of epiparasitism rise likewise. Thus, given a hundred hosts, by the time that the parasite has laid ten eggs, there is an even chance that one will have been placed in a host already infected, and so on, until with fifty eggs the odds are even that no less than ten ovipositions will have been duplicated in this way. But although hyperparasitism may have arisen from epiparasitism, through metaparasitism, primary parasitism cannot be accounted for thus.

Wheeler (**15**) has put forward a theory of the origin of parasitism in the Aculeata. He supposes that parasitism arose within the species, when certain individuals acquired the habit of laying their eggs in the brood cells of their neighbours, instead of working for themselves: and he supports his suggestion by the significant fact that the existing parasites are frequently generically allied to the host species.

But this theory can hardly be extended to the Parasitica, even if we regard them as a heterogeneous group, derived from different ancestral stocks, and classified together in virtue of characters acquired independently by members of different families in adaptation to parasitic life. The existing Parasitica are a vast class, of infinite variety of size, structure, and habit; and with the exception of most of the Cynipids and a few Chalcids, which are gall-formers on plants, all are parasitic upon insects, frequently upon families distantly related to them.

To suppose that the parasitic habit arose spontaneously in a common ancestor, and was perpetuated by natural selection, involves the assumption of a considerable initial mutation. If, as among the bees and wasps, we found that phylogenetic relationship between host and parasite was the usual rule, we might suppose that parasitism arose within the species in the Parasitica, as Wheeler suggests for the Aculeata; but there is as much to be said against as for this view, since the modern Parasitica include, not only their own allies, but almost every stage of almost every family of insects among their hosts.

Nevertheless, parasitism must have had a beginning, and the suggestion may be put forward that the parasitic habit arose among these Hymenoptera from the inquiline habit. In other words, the proto-Parasitica were phytophagous, and oviposited on plants. A further stage was reached, when, for the better protection of the eggs, they resorted to the shelter of galls and other deformities produced by members of their own tribe, and by other insects. Here they became established as commensals or inquilines, and from the inquiline habit to the parasitic habit is possibly not a great step. The Chalcid, Torymus propinquis, previously alluded to, is now an ectoparasitic of a gall-forming Cecidomyiid of the nettle, but if this view is correct, its ancestors inhabited this, or a similar gall, as inquilines, and later acquired the habit of devouring the maker of the growth that harboured them.

The intra-specific origin of parasitism in bees may find a parallel among inquilines, for it is quite conceivable that certain individuals may have adopted the habit of ovipositing in a ready-formed gall, and thus became inquilines to their own species. Cameron (**2**) remarks that among the Cynipidae, the known inquilines are species of Synergus, Ceroptres, or Sapholytus, which are all forms nearly related to the true gall-formers.

The view that parasitism is derived from inquilinism would account for the diversity of the hosts of the Parasitica. Galls, and similar plant deformities, are caused by insects of other groups, such as many Hemiptera, Diptera, and Lepidoptera. The ancestors of the Parasitica may have used these as well as the galls produced by members of their own family, and later become parasitic upon the insects which formed them.

It will be very desirable in future to investigate fully the bionomics of the forms reared from, for example, Cynipid galls. If any, generally found to be inquiline, are proved on occasion to devour the maker of the gall, it will support the suggestion that the Parasitica are descended from inquiline ancestors.

SUMMARY.

1. Asaphes vulgaris, Wlk., Pachycrepis clavata, Wlk., and Pachyneuron, sp., are hyperparasites of aphides through the larvae of certain Braconidae (Aphidius).
2. Oviposition took place after mating for Asaphes and Pachycrepis, and parthenogenetically for Pachyneuron.
3. The eggs are deposited upon the body of the host when the latter is fully fed and about to undergo metamorphosis within the skin of the aphide.
4. The larvae feed ectoparasitically upon the host, which soon becomes a decomposing mass.

5. The newly-hatched larvae are maggot-shaped forms, with four pairs of open spiracles and two cephalic papillae.

6. In the later stages small tubercles are developed on the prothorax and succeeding segments, and there are ten pairs of functional spiracles.

7. The total period of development is a little over three weeks, and at least two broods may occur in the summer.

8. The bionomics of aphides and of their parasites and hyperparasites are discussed.

9. The term ' epiparasitism ' is proposed instead of ' superparasitism ' which has been used by other writers, and it is suggested that it should be restricted to cases where two or more species, or two or more individuals of the same species, independently attack the same host.

10. The term ' metaparasitism ' is suggested for cases where one parasite or hyperparasite in epiparasitism, becomes secondarily hyperparasitic upon the other.

11. Instances are given of the occurrence of epiparasitism and metaparasitism among other hymenopterous parasites.

12. The origin of parasitism in the Hymenoptera parasitica is discussed, and it is suggested that it arose from an earlier inquiline mode of life.

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